Evolving eco-system: a network of networks

Debashish Chowdhury[1] and Dietrich Stauffer[2]

Department of Physics, Indian Institute of Technology, Kanpur 208016, India

Institut for Theoretical Physics, Cologne University, D-50923 Köln, Euroland

E-mail: debch@iitk.ac.in, stauffer@thp.uni-koeln.de

Abstract

Ecology and evolution are inseparable. Motivated by some recent experiments, we have developed models of evolutionary ecology from the perspective of dynamic networks. In these models, in addition to the intra-node dynamics, which corresponds to an individual-based population dynamics of species, the entire network itself changes slowly with time to capture evolutionary processes. After a brief summary of our recent published works on these network models of eco-systems, we extend the most recent version of the model incorporating predators that wander into neighbouring spatial patches for food.

Keywords: Food web, Monte Carlo simulation, Self organization,

1   Introduction

An eco-system may be viewed as a functional network of species; the food web [1] corresponding to the eco-system consists of nodes and links where each node corresponds to a species and the (directed) links represent the prey-predator interactions such that the direction of the link indicates the direction of flow of nutrient (i.e., *from* a prey *to* one of its predators) [2, 3]. For convenience, most of the earlier ecological models that describe population dynamics, usually ignored macro-evolutionary changes in the eco-system and, therefore, assumed the food web to be independent of time. On the other hand, most of the macro-evolutionary models [4, 5] of speciation and extinction of species did not explicitly explore the ageing and age-distributions of the populations of various species in the system. The models of ageing, usually, focus on only one single species.

But, recent experimental evidences [6, 7, 8] have established that significant evolutionary changes can occur over ecologically relevant time scales. Motivated by these experiments, we have developed models [9, 10, 11, 12, 13] of evolutionary ecology from the perspective of dynamic networks. In these models, in addition to the intra-node dynamics, which corresponds to population dynamics of species, the entire network itself changes slowly with time to capture evolutionary processes. The aim of these models is to provide insight into the

mechanisms that give rise to the generic features of the biological evolution of real eco-systems.

In this paper, after a brief review of the earlier network models, including our own [9, 10, 11, 12], we extend the most recent version [13] of our model by allowing predators to prey on species in the neighbouring spatial patches as well.

2   Earlier network models

A network model of ecosystems was developed by Sole and Manrubia [14]. The state of the i-th species $(i = 1, 2, ...N)$ is represented by a two-state variable S_i; $S_i = 0$ or 1 depending on whether it is extinct or alive, respectively. The inter-species interactions are captured by the interaction matrix $\mathbf{J}$; the element J_{ij} denotes the influence *of* the species j *on* the species i. If $J_{ij} > 0$ while, simultaneously, $J_{ji} < 0$ then i is the predator and j is the prey. On the other hand, if both J_{ij} and J_{ji} are positive (negative) they the two species cooperate (compete). The food web in the Sole-Manrubia model [14] has a random architecture.

The dynamics of the system consists in updating the states of the system in three steps. At the first step, one of the input connections J_{ij} for each species i is picked up randomly and assigned a new value drawn from the uniform distribution in the interval $[-1, 1]$, irrespective of its previous magnitude and sign. At the second step, the new state of each of the species is decided by the equation

$$S_i(t+1) = \Theta\left(\sum_{j=1}^{N} J_{ij}S_j(t) - \theta_i\right) \tag{1}$$

where θ_i is a threshold parameter for the species i and $\Theta(x)$ is the standard step function. If $S(t+1)$ becomes zero for m species, then an extinction of size m is said to have taken place. Finally, at the third step, all the niches left vacant by the extinct species are refilled by copies of one of the randomly selected non-extinct species. Sole and Manrubia [14] observed that the distributions of the sizes of these extinctions could be fitted to a power law of the form $N(m) \sim m^{-\alpha}$ with an exponent $\alpha \simeq 2.3$.

Abramson [15] considered a linear food web which is extremely unrealistic and required a constant number of species. Amaral and Meyer [16] considered a hierarchical food web but the population dynamics was oversimplified. The main limitation of these network models is that the individual organisms do not appear explicitly.

3   The "unified" network model

We represent the spatial extensions of the eco-system by a square lattice where each site represents a spatial "patch" (see the left side of Fig.1). Moreover, a
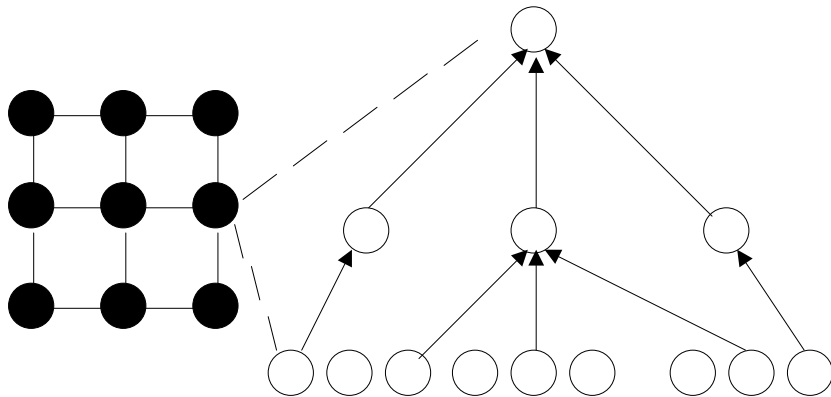
Figure 1: A schematic representation of the eco-system by a network of networks. Each filled circle in the left part, representing a spatial "patch" of the eco-system, is endowed with a hierarchical network, shown in the right part, that graphically represents the food web structure.

food web is assigned to each spatial "patch" (see the right side of Fig.1). Thus, the eco-system can be modelled as a *network of networks* (see Fig.1).

As in our earlier papers [10, 11, 12, 13], we assume a generic *hierarchical* architecture of the food web, where niches are arranged in different trophic levels ℓ $(1 \leq \ell \leq \ell_{max})$, with no more than $m^{\ell-1}$ nodes in each level (m is a positive integer). Species in level ℓ can prey on (or ignore) species on the immediately lower level $\ell + 1$. The total number of species cannot exceed $N_{max} = (m^{\ell_{max}} - 1)/(m - 1)$, the total number of nodes. Note that ℓ_{max} and m (and, therefore, N_{max}) are time-independent parameters in the model. At any arbitrary instant of time t the model consists of $N(t)$ *species* each of which occupies one of the nodes of the dynamic network. Our model allows $N(t)$ to fluctuate with time over the range $\ell \leq N(t) \leq N_{max}$.

Following the spirit of the Sole-Manrubia model [14] we describe the prey-predator interaction by the elements of the interaction matrix J, except that, for simplicity, we allow only the discrete integer values $J_{ij} = \pm 1, 0$.

The food web itself evolves slowly over sufficiently long time scales. In order to capture the changing food habits, each of the species in our model re-adjusts, with the probability p_{mut}, a link J from one of its predators and another to one of its potential preys at every time step [14]. Moreover, random genetic mutations are captured also by implementing random tinkering of some of the intra-node characteristics which will be introduced below. Furthermore, even the occupants of the nodes can change with time because, following extinction, the vacant nodes are slowly re-occupied through speciation, to be explained below.

Population dynamics at the neighbouring patches are coupled by *migration*: a population may expand into a neighbouring lattice site, if the population there is

zero for the same species on the same level. A direct inter-"patch" interaction enters through the wandering of the predators into neighbouring patches for food: a species at a patch i, j can prey on species at the next lower level in the food web located the neighbouring patches $i \pm 1, j$ and $i, j \pm 1$ as well as those at the same location, namely, i, j.

The *intra*-species competitions among the organisms of the same species for limited availability of resources, other than food, imposes the upper limit n_{max} of the allowed population of each species. The population (i.e., the total number of organisms) of a given species, say, i, in the spatial patch α at any arbitrary instant of time t is given by $n_{i,\alpha}(t) \leq n_{max}$. Thus, the total number of organisms $n(t)$ in the eco-system at time t is given by $n(t) = \sum_{i=1}^{N(t)} \sum_{\alpha} n_{i,\alpha}(t)$.

For simplicity, we assume the reproductions to be *asexual*. At each time step, the survivors give birth to M offspring with probability

$$p_{birth} = [(X_{max} - a)/(X_{max} - X_{rep})][1 - n/n_{max}]$$

if their age a is above the minimum reproduction age X_{rep}.

We assume that each individual either ages by one time unit for each time step, or it dies. In addition to the possibility of death as prey, the probability of natural death of each organism of age a is assumed to be given by

$$p_{death} = \exp[(a - X_{max})r/M]$$

where X_{max} is the maximum possible age and M is the litter size of the whole species; where r is a free parameter, e.g. 0.05. (For ages below the minimum reproduction age X_{rep} the death probability is assumed to be age-independent, with a replaced by X_{rep} in the above equation.)

During each time step, because of random genetic mutations, X_{rep} and M independently increase or decrease by unity, with equal probability, p_{mut}. X_{rep} is not allowed to exceed a X_{max} of this species, while M is restricted to remain positive.

The J account not only for the *inter*-species interactions but also *intra*-species competitions for food. Let S_i^+ be the number of all prey individuals for species i on the lower trophic level, and S_i^- be m times the number of all predator individuals on the higher trophic level. Because of the larger body size of the predators, we assume that a predator eats m prey per time interval. Then, S_i^+ gives the available food for species i, and S_i^- is the contribution of species i to the available food for all predators on the next higher level. If $n_i - S_i^+$ is larger than S_i^- then food shortage will be the dominant cause of premature death of a fraction of the existing population of the species i. On the other hand, if $n_i - S_i^+ < S_i^-$, then a fraction of the existing population will be wiped out primarily by the predators.

Because of the natural death mentioned above and, more importantly, prey-predator interactions, the populations of some species may fall to zero. In order to capture the process of *speciation*, all the empty nodes in a trophic level of the network are re-filled, with a probability p_{sp}, by random mutants of *one common ancestor* which is picked up randomly from among the non-extinct species at
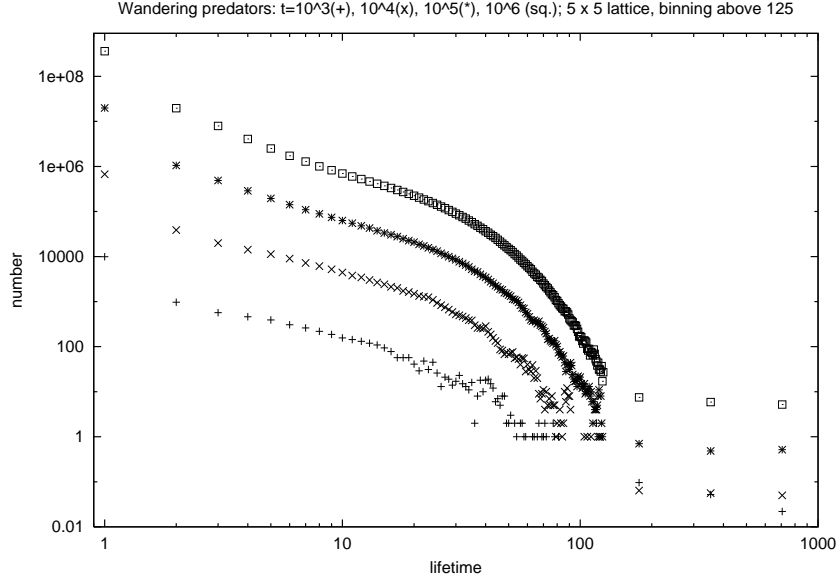
Figure 2: Log-log plots of the distributions of the lifetimes of the species. The common parameters for all the curves are $m = 2$, $p_{lev} = 0.001$, $p_{sp} = 0.1$, $p_{mut} = 0.001$, $C = 0.2, r = 0.05$. The symbols $+, \times, *$ and the unfilled square correspond to $t = 10^3, 10^4, 10^5, 10^6$ on a 5×5 square lattice.

the same trophic level. The subsequent accumulation of random mutations over sufficiently long time leads to the divergence of the genomes of the parent and daughter species that is an essential feature of speciation.

However, occasionally, all the niches at a level may lie vacant. Under such circumstances, all these vacant nodes are to be filled by a mutant of the non-extinct species occupying the closest *lower* level. In our computer simulations, the search for this non-extinct species is carried out in steps, if even the lower level is also completely empty, the search for survivor shifts to the next lower level and the process continues till the lowest level is reached. The species at the lowest level (representing, for example, plankton) are assumed to be immortal. In order to capture the fact that real ecosystems can exhibit growing bio-diversity over sufficiently long period of time, we allowed adding a new trophic level to the food web, with a small probability p_{lev} per unit time, provided the total bio-mass distributed over all the levels (including the new one) does not exceed the total bio-mass available in the eco-system. Increase of the number trophic level means the diversification at the erstwhile topmost level as well as all the lower levels and the emergence of yet another dominating species that occupies the new highest level.

4   Results and conclusions

The average distributions of the lifetimes of the species are plotted in fig.2. It is not possible to fit a straight line through the data over the entire range of lifetimes; only a limited regime is consistent with a power-law with the effective exponent 2, which has been predicted by several models of "macro"-evolution [2, 3]. This qualitative behaviour is similar to those observed earlier with simpler versions of our "unified" model, except for the new feature that a plateau appears in the Fig2 for lifetimes $\gg 100$.

Because of the various known limitations of the available fossil data, it is questionable whether real extinctions follow power laws and, if so, over how many orders of magnitude.

In summary, we have extended the most recent version of our model "unified" model of evolutionary ecology [9, 10, 11, 12, 13], formulated as a network of networks, by incorporating predator-prey interactions among species on neighbouring spatial patches. This improvement does not alter the qualitative features of the statistics of extinctions in our "unified" model.

References

[1] B. Drossel and A. J. McKane, in: *Handbook of Graphs and Networks - From the Genome to the Internet*, eds. S. Bornholdt, and H. G. Schuster, (Wiley-VCH, Weinheim, 2003).

[2] B. Drossel, Adv. Phys. **50**, 209 (2001).

[3] M. E. J. Newman and R. G. Palmer, *Modeling Extinction*, (Oxford University Press, New York, 2002).

[4] P. Bak and K. Sneppen, Phys. Rev. Lett. **71**, 4083 (1993).

[5] R. V. Sole, in: *Statistical Mechanics of Biocomplexity*, eds. D. Reguera, J. M. G. Vilar and J. M. Rubi, Lec. Notes in Phys. vol.527, 217 (Springer, 1999) and references therein.

[6] J.N. Thompson, Science **284**, 2116 (1999).

[7] C.A. Stockwell, A.P. Hendry and M.T. Kinnison, Trends in Ecology and Evolution, **18**, 94 (2003).

[8] T. Yoshida, L.E. Jones, S.P. Ellner, G.F. Fussmann and N.G. Hairston Jr., Nature, **424**, 303 (2003).

[9] D. Chowdhury, D. Stauffer and A. Kunwar, Phys. Rev. Lett. **90**, 068101 (2003).

[10] D. Chowdhury and D. Stauffer, Phys. Rev. E **68**, 041901 (2004).

[11] D. Stauffer and D. Chowdhury, Physica A, **336**, 102 (2004).

[12] D. Chowdhury and D. Stauffer, Physica A, (in press).

[13] D. Stauffer, A. Kunwar and D. Chowdhury, e-print q-bio.PE/0403040; A. Kunwar, to be published.

[14] R. V. Solé and S. C. Manrubia, Phys. Rev. E **54**, R42 (1996); **55**, 4500 (1997).

[15] G. Abramson, Phys. Rev. E **55**, 785 (1997).

[16] L.A.N. Amaral and M. Meyer, Phys. Rev. Lett. **82**, 652 (1999).